Nota Lepi. **44** 2021: 29–56 | DOI 10.3897/nl.44.52350 Research Article

New taxa of extant and fossil primitive moths in South-East Asia and their biogeographic significance (Lepidoptera, Micropterigidae, Agathiphagidae, Lophocoronidae)

Wolfram Mey[1], Théo Léger[1], Vu Van Lien[2]

1 *Museum für Naturkunde, Leibniz Institute of Evolution and Biodiversity Research, Invalidenstr. 43, 10115 Berlin, Germany; wolfram.mey@mfn.de, Theo.Leger@mfn.berlin*

2 *Vietnam National Museum of Nature, Hanoi, Vietnam; vulien@vnmn.vast.vn*

http://zoobank.org/FC32D2F4-5EE1-4484-8BAF-D873487DB332

Received 23 March 2020; accepted 15 October 2020; published: 10 March 2021
Subject Editor: David C. Lees.

Abstract. We report some surprising recent distributional range extensions of one extant genus and two more families of primitive moths discovered in amber fossils from South-east Asia which were previously only known from Australia and/or the southwestern Pacific, with the possible exception of an undescribed Siberian fossil attributed to Lophocoronidae. During entomological field work in rain forests of central Vietnam a new species of Micropterigidae was discovered. It is described herein as *Aureopterix bachmaensis* sp. nov. based on male and female specimens collected at light in the Bach-Ma National Park. The identification was corroborated by a molecular analysis. This is the first record of this genus in the Northern Hemisphere, previously thought to be restricted to the Australian Region (including New Caledonia). First results of investigations of Burmese amber inclusions now reveal the presence of the Australian Region families Agathiphagidae and Lophocoronidae in the Cretaceous of Asia. The fossil taxon *Agathiphagama perdita* gen. nov., **sp. nov.** is established on the basis of two females and this is assigned to Agathiphagidae. The fossil genus *Acanthocorona* gen. nov. is established in Lophocoronidae and includes seven species described here as *A. skalskii* **sp. nov.**, *A. bowangi* **sp. nov.**, *A. muelleri* **sp. nov.**, *A. kuranishii* **sp. nov.**, *A. sattleri* **sp. nov.**, *A. spinifera* **sp. nov.** and *A. wichardi* **sp. nov.** The new species can be distinguished by the male genitalia which are illustrated together with wing venation and other morphological characters. The disjunct ranges of these taxa are discussed in a historical biogeographic context. Vicariance and dispersal hypotheses explaining the disjunct pattern are discussed. The discovery of these new species suggests a broader ancestral range of *Aureopterix*, Agathiphagidae and Lophocoronidae. Their extant ranges may be regarded as remnants or relicts of a wider distribution in the Mesozoic, or at least in the case of *Aureopterix* they could be the results of recent or ancient dispersal processes, since the calibration of molecular splits does not so far accord with plate tectonics.

Introduction

In continental South-East Asia the faunas of the Eastern Palaearctic and Oriental Regions share a common border. This borderline is not a clear-cut delimitation and separation of both faunas, but rather a broad transition zone extending from the slopes of the southern Himalayas in northern India to northern Myanmar, Thailand, Laos, Vietnam and southern China including Taiwan (Müller 1981).

This zone includes biodiversity hotspots for many insect groups (Balian et al. 2008; Konstantinov et al. 2009) and is also seen as a diversity centre of vascular plants (Barthlott et al. 1999). It does not simply combine taxa from different biomes, but is also home of a great number of endemic species. The existence of these species might be evidence of an enduring ecological stability and favourable conditions facilitating both the evolution of recent neo-endemics and the persistence of older palaeo-endemics (Fjeldså and Lovett 1997). Taxa belonging to old lineages dating back to the Mesozoic are of particular interest. In Lepidoptera, the following genera of homoneurous families, which represent these lineages, were documented with autochthonous species occurring in the area to date (Meyrick 1909; Issiki 1931; Issiki and Stringer 1932; Hwang 1965; Mutuura 1971; Davis et al. 1995; Mey 1997; Hashimoto and Mey 2000; Chen et al. 2009; Hirowatari et al. 2009; Lees et al. 2010):

Micropterigidae: *Micropterix* Hübner, 1825, *Paramartyria* Issiki, 1931, *Vietomartyria* Hashimoto & Mey, 2000
Eriocraniidae: *Eriocrania* Zeller, 1850, unpublished record (in coll. MfN)
Hepialoidea: *Ogygioses* Issiki & Stringer, 1932
Neopseustidae: *Neopseustis* Meyrick, 1909, *Nematocentropus* Hwang, 1965

A common feature of primitive moths is the low number of collected specimens for the majority of species. The species are rarely encountered in nature, and almost every new record merits communication. The scarcity of hitherto found specimens, however, suggests the occurrence of further relict species. Concerning Microlepidoptera, continental South East Asia has not been sufficiently explored, and new discoveries remain to be made, particularly in the mountain ranges of the Palaearctic-Oriental transition zone.

During the first field trip of the joint Vietnamese-German project VIETBIO to Central Vietnam in 2018, the first author was searching for caddisflies and micromoths in the Bach-Ma National Park (Mey et al. 2020). A single micropterigid female was collected at lights on 10.06.2018. Intensive searching at the locality for additional specimens yielded no results. Two days later, collecting in a different valley of the National Park, the corresponding male was found, again at the lights. Previous records of Micropterigidae were restricted to the north of Vietnam (Mey 1997), and the family was not expected to occur in the south.

Closer inspections of the specimens identified them as belonging to *Aureopterix* Gibbs, 2010, a genus reported so far only from Australia and New Caledonia (Gibbs 2010). Though similar in morphology to the two hitherto described species, the Vietnamese specimens represent a new, distinct species for this genus, which is described herein.

Examination of insect inclusions in Burmese amber resulted in the discovery of individuals which were identified as putative species of Agathiphagidae and Lophocoronidae. Both families are currently regarded as extant, endemic families of Australia and Southwest Pacific Islands. Interestingly, Skalski (1979) has tentatively determined a fossil individual from Siberian amber (Tajmyr region) of Upper Cretaceous (Santonian) as a representative of Lophocoronidae. The species was, however, not formally described and named. Burmese amber originates predominantly from the Hukawng Valley near Myitkyina, Kachin State, Myanmar (Fig. 1). It derives from an amber-bearing layer, which is not exposed at the surface but extends to a depth of 2–15 m (Cruickshank and Ko 2003). The amber deposits have been dated in detail by Shi et al. (2012). The age determination is of early Cenomanian (98.8 ± 0.6 Ma) given by U-Pb dating of zircons from the volcanoclastic

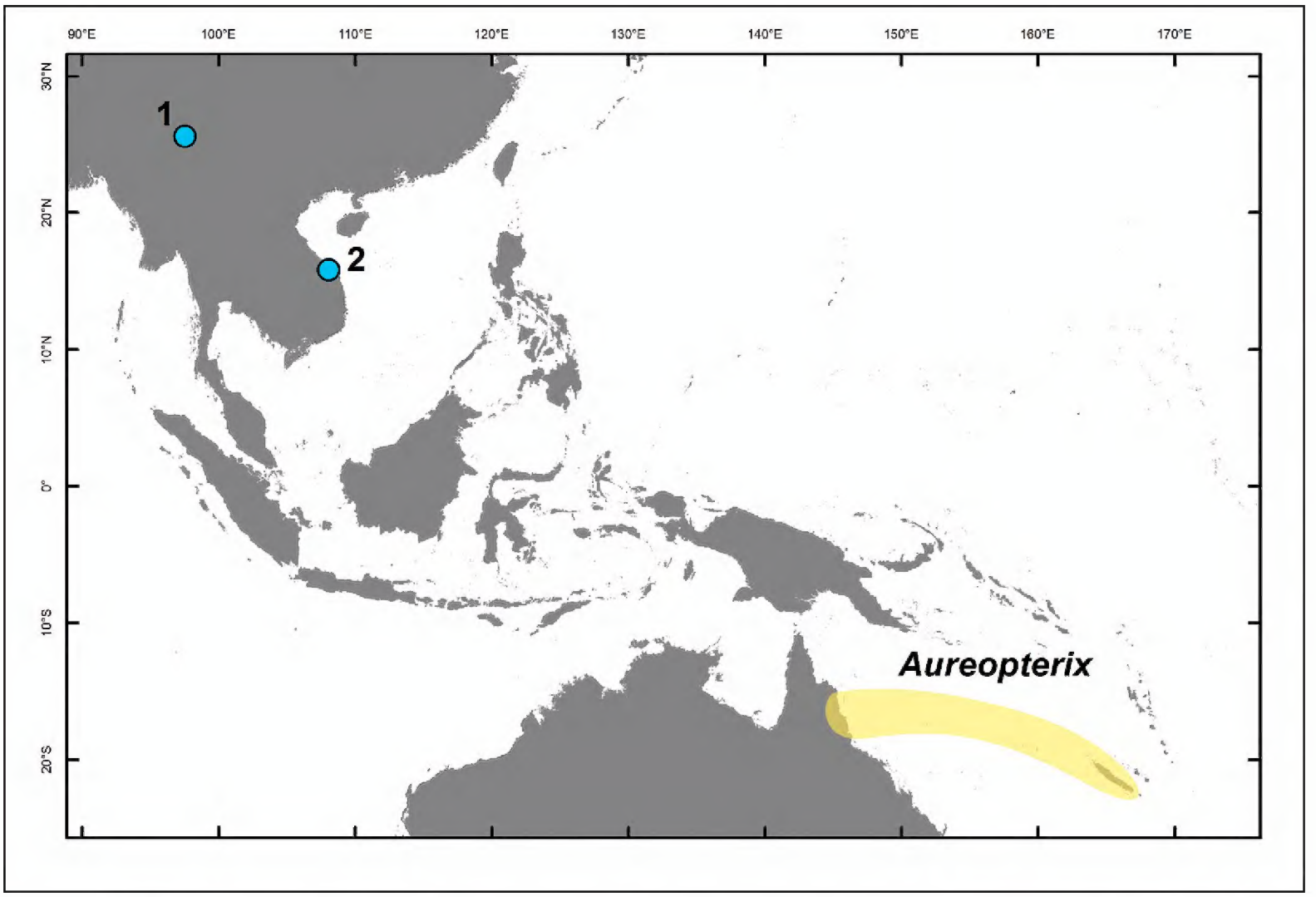


Figure 1. Map of the distribution of *Aureopterix* Gibbs, 2010 with disjunct ranges in Vietnam and (in yellow) Australia/New Caledonia, and locality of Burmese amber mines (**1.** Mine in Hukawng Valley, Kachin State, Myanmar; **2.** New record of *Aureopterix*, Bach-Ma National Park, Vietnam).

matrix of the amber (Shi et al. 2012). The first synopsis of identified biota from Burmese amber was published by Grimaldi et al. (2002). A regularly updated catalogue of described taxa is available online (Ross 2019). There are only a few species of Lepidoptera described from this class of amber (Sohn et al. 2012). Representatives of the family Micropterigidae were encountered quite often in inclusions, and therefore, led to the descriptions of five species (Zhang et al. 2017; Cockerell 1919) which were assigned to the extant genus *Sabatinca* (Walker, 1863). One species was described in Douglasiidae, a placement (Poinar 2019a) that needs to be confirmed. These are the only available descriptions of Burmese amber Lepidoptera. The Burmese amber, however, contains a diverse and rich fauna of Microlepidoptera of ancient and more derived forms, which are currently under investigation and documentation (see Mey 2019). The following descriptions are some first results and are included in this article for providing a biogeographical context in the discussion on the unexpected discovery of *Aureopterix bachmaensis* sp. nov. in Vietnam.

Material and methods

Extant taxa

The adult moths were pinned and set in the field. Genitalia drawings were performed prior to embedding in Euparal on a genitalia slide. A camera lucida attached to a Leica MZ12 compound microscope was used. Genital preparations were made according to the procedure described in

Robinson (1976). The genitalia were embedded in Euparal. Chlorazol Black was used to stain the membranous parts of the genitalia. Photographic documentation of imagines was done with a Leica Z 16 APOA Microscope in combination with a Leica DFC490 camera and Leica Application Suite programme, version 4.5.0 on a Windows PC. The map (Fig. 1) was produced with ArcGIS software.

DNA extraction and sequencing

DNA extraction were performed with a NucleoSpin Tissue kit (Macherey-Nagel, Düren, Germany). The standard forward and reverse primers LCO/Nancy for the DNA barcode region failed at amplifying the target region. The COI barcode was thus amplified in two parts refered to as COI fragment 1a and 1b, using primers from Léger et al. (2020). PCR-mix consisted of 17.8 µl ddH_2O, 2.5 µl 10× Puffer, 1 µl Mg (25 mM), 0.5 µl dNTP Mix, 0.5 µl of each primer, 0.2 µl of Taq polymerase (New England Biolabs, Ipswich, USA) and 2 µl of the DNA sample, totalling a volume of 25 µl. PCR program was that of Léger et al. (2020). PCR product cleaning and sequencing were performed by MACROGEN (Netherlands).

Sequence analysis

Sequences were eye-checked under PhyDE 0.9971 (Müller et al. 2005), also aligned visually with other DNA barcode sequences of *Aureopterix* and *Sabatinca* retrieved from BOLD (http://v4.boldsystems.org/). Phylogenetic analyses were performed on RAxML on the CIPRES portal (Miller et al. 2010), with Rapid Bootstrap Search stopped after 252 replicates. K2P distances were calculated on MEGA X (Kumar et al. 2018).

Fossil taxa

Photos of fossil species were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 80D, EOS utility software and the Zerene Stacker software.

The fossils were examined under incident and transmitted light using a stereomicroscope (Leica MZ125). Line drawings were produced with a Leica camera lucida and digitally processed using Adobe Photoshop CS4. Measurements were made with the ocular micrometer of the stereomicroscope.

All taxonomic acts established in the present work have been registered in ZooBank, together with the electronic publication: http://zoobank.org/FC32D2F4-5EE1-4484-8BAF-D873487DB332.

The terminology of genitalia structures used in the descriptions of taxa follows Gibbs (2010) for Micropterigidae, Kristensen (1998) for Agathiphagidae and Nielsen and Kristensen (1996) for Lophocoronidae. For each of these families a separate superfamily taxon was established (see Kristensen and Skalski 1998). The use of these names was found to be dispensable here, because they provide no additional information for the families and the taxonomic contents of the present article.

Abbreviations of depository collections:

AMNH	American Museum of Natural History, New York
TF	ex coll. Thilo Fischer, München
PM	ex coll. Patrick Müller, Käshofen (will be transferred to MfN later)
MfN	Museum für Naturkunde, Berlin
NIGP	Nanjing Institute of Geology and Palaeontology, Nanjing, P.R. of China
VNMN	Vietnam National Museum of Nature, Hanoi.

Systematic account

Micropterigidae

Aureopterix bachmaensis sp. nov.

http://zoobank.org/59D2AADB-5BBF-4F8D-BED4-C7B9F2FF1964

Figs 1–11

Type material. ***Holotype*** ♂, Vietnam, Thua Thien-Hue Province, Bach-Ma National Park, 12.vi.2018, above Rhododendron Trail, 1256 m, 16°11.757'N, 107°50.922'E, at light, leg. W. Mey, genitalia slide Mey 08/20, DNA voucher Lepidoptera, MFN LEP042 (VNMN).

***Paratypes*:** 2 ♀, Vietnam, Thua Thien-Hue Province, Bach-Ma National Park, 10.vi.2018, Five Lakes Trail, 1190 m, 16°12.214'N, 107°50.441'E, at light, leg. W. Mey, genitalia slide Mey 09/20, 1 ♀ in alcohol, DNA voucher Lepidoptera, MFNLEP041 (MfN).

Etymology. The specific name is derived from the name of the Bach-Ma National Park.

Diagnosis. Vietnam. Male with long genitalia, projecting half the length of abdomen in dried specimens; abdomen and genitalia with long, scattered setae; tergum X of males with single setal tuft on each ventro-lateral margin on a raised base at mid-length.

Forewing ground colour and fascial pattern (Figs 1, 2) corresponding widely with the two other known species of *Aureopterix* Gibbs, 2010. The male genitalia of the new species are more similar to those of *A. micans* Gibbs, 2010, described from New Caledonia, and less similar to *A. sterops* (Turner, 1921) distributed in northern Queensland, eastern Australia. *A. bachmaensis* sp. nov. mainly differs from both species by the shape of the valvae and the slender segment X bearing one single setal brush on a knob-like process of the lateral margin in male genitalia.

Description. (Figs 3–6) Length of forewings 3.9 mm (male) to 4.1 mm (females). Antennae with 34 flagellomeres in male, 32 in female, extending to two-thirds of forewings; first four basal flagellomeres fused, clothed with white lamellar scales, following flagellomeres brown, with long, dark sensillae and ascoids, female flagellomeres 4 to 6 black; head capsule dark brown, with dense tufts of white, piliform scales on frons and vertex; eyes hemispherical; epicranial suture and ocelli absent; clypeus separated from frons by a deep, arched suture extending between the tentorial pits; labrum long, triangular with rounded tip; mandibles present, apical portions hidden under labrum; maxillae with long, five-segmented palpi, held in vertical position close to frons, inner endites two short, rounded processes (= galea and subgalea); labial palpi short, three-segmented, terminal segment with a garland of stiff sensillae. Pronotum and basal part of tegulae brown, dorsum of thorax with silvery white, lamellar scales. Ground colour of forewings pale white, shining silvery, some brown spots at base of costa, apical part of forewings with oblique, bronzy fascia, fringes white, hindwings shining bronzy on upper- and underside. Wing venation (Fig. 7) with Sc and R1 forked in forewing, simple in hindwing or absent (R1), R4 and R5 in both wings very short, forming forks encompassing the wing tips, hindwings with accessory cell absent, anal veins without looping. Wing coupling mechanism with short jugum of forewings and bundle of three erect bristles on costal base of male hindwings, females without those bristles. Legs with white coxae and femora, tibiae and tarsal segments dark brown, epiphysis present on foretibia, legs clothed with acute tipped scales, long or short spines in addition to spurs absent, spurs 0.0.4. Male abdomen with long bristles on ventral side, glands of sterna V present, orifice rounded, segment VIII of male present as tergum only, no traces of sternite visible.

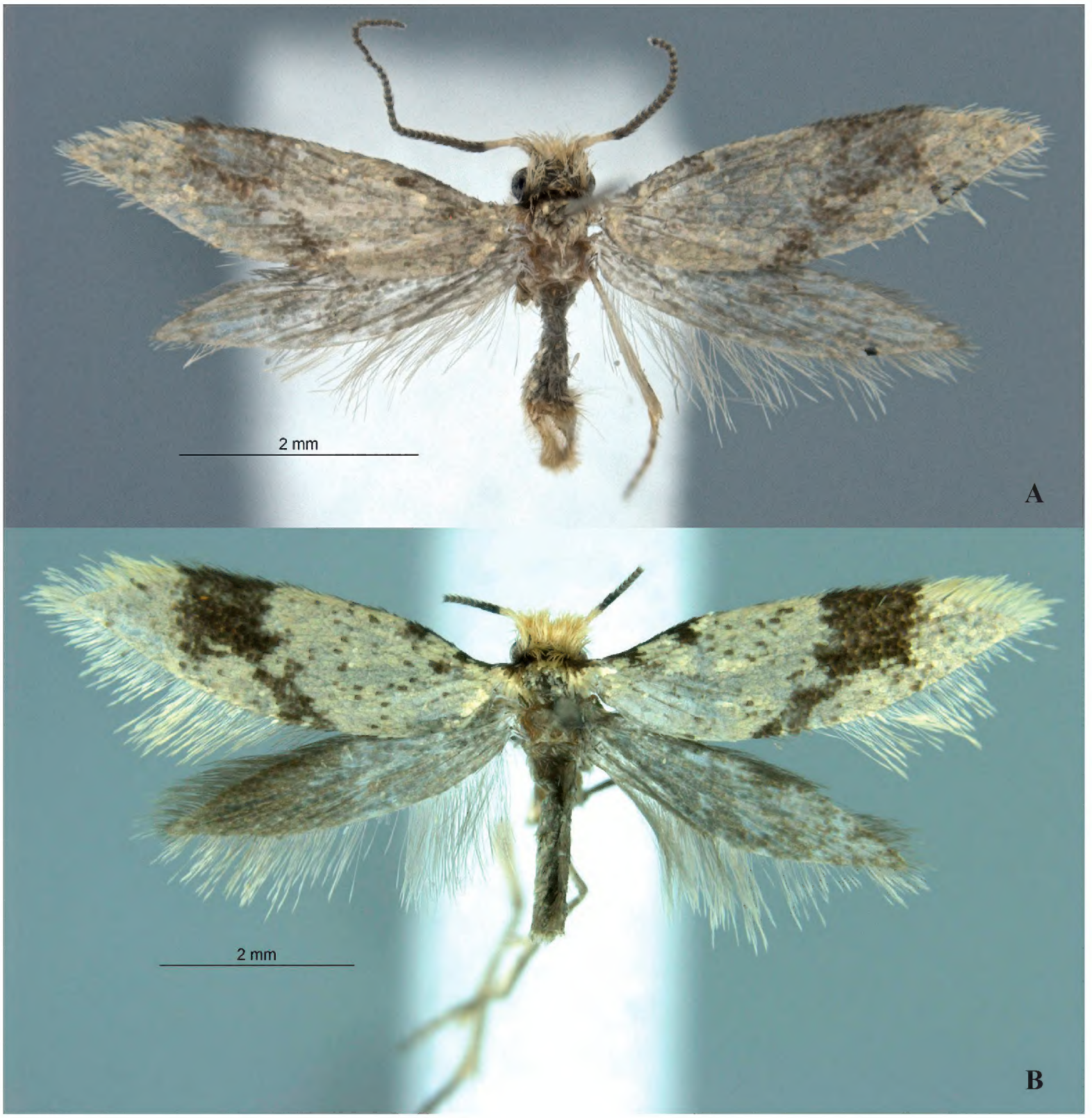
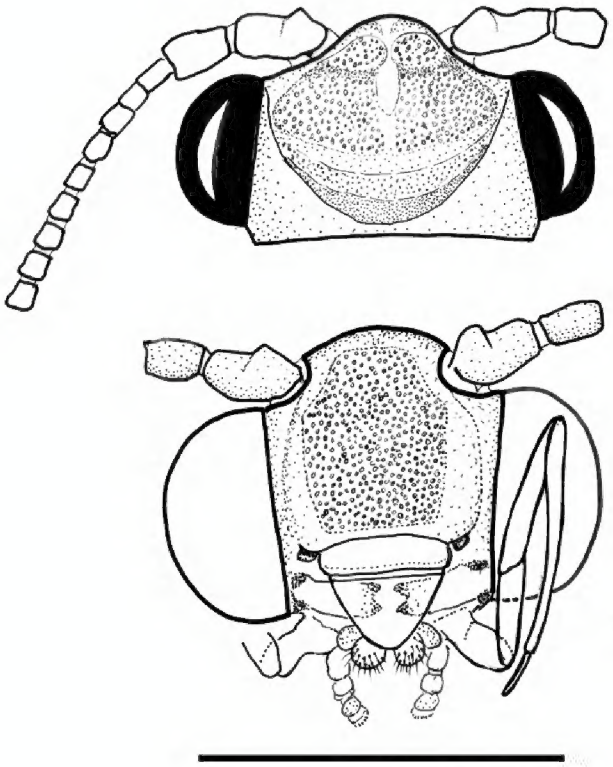
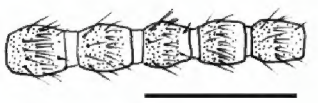


Figure 2. Adults of *Aureopterix bachmaensis* sp. nov. and their phylogenetic placement. **A.** Male, holotype; **B.** Female, paratype; **C.** Phylogenetic tree of *Aureopterix*. Best scoring RAxML-tree with node calibration in millions of years displayed above branches. *Sabatinca* branch not represented for visual convenience.



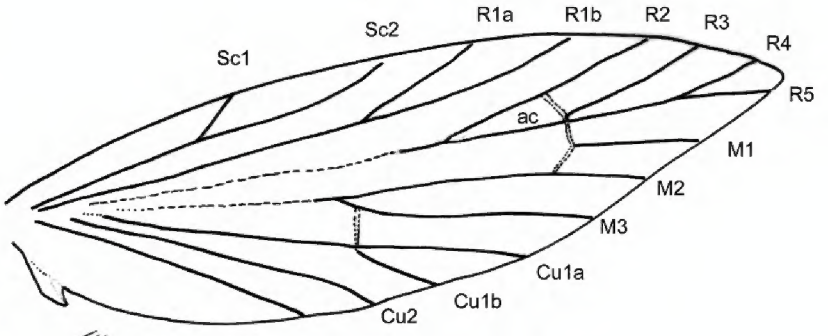
3

5

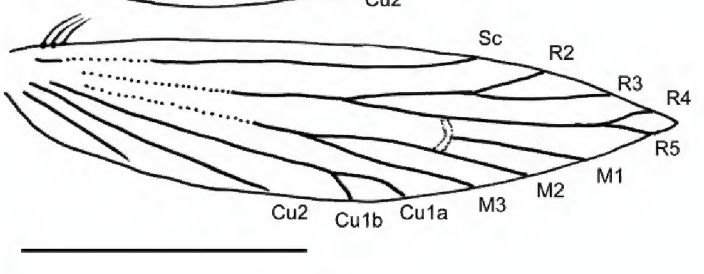


6

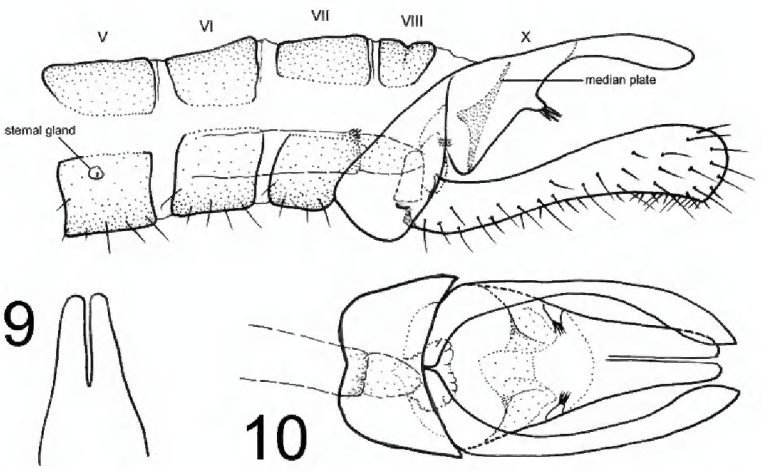
4



7

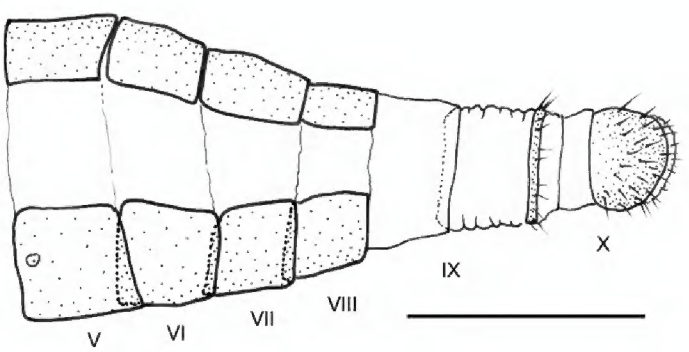


8



9

10



11

Figures 3–11. *Aureopterix bachmaensis* sp. nov.; **3–5.** Head, female; **3.** Dorsal view; **4.** Frontal view, right maxillary palpus omitted; **5.** Lateral view; **6.** Flagellomeres, mid-section; **7.** Wing venation, holotype; **8.** Male abdomen and genitalia, lateral view; **9.** Segment X, dorsal view; **10.** Male genitalia, ventral view; **11.** Female abdomen, lateral view. Scale bars: 0.25 mm (**3–5.**); 10 µm (**6.**); 1 mm (**7.**); 0.5 mm (**8.**); 0.5 mm (**10., 11.**);

Male genitalia (Figs 8–10): segment IX bulbous, not forming a closed ring, anterior margin of ventral side slightly excavated, valvae very long, club-shaped, tips acute in ventral view; segment X shorter than length of valvae, narrowly cleft at apex for half of its length, paired apices rounded, lateral margin with a brush of 3–4 short setae on a short process directed ventro-mediad; median plate weakly sclerotized, enclosed in basal part of segment X; phallic apparatus long and tubular, terminal part of phallocrypt with micro-spines on dorsal side, distal part of phallus membranous, cornuti absent.

Table 1. K2P distances between DNA barcode sequences of *Aureopterix* species. GenBank accession numbers are appended to each sample.

Species	MFNLEP41	MFNLEP42	MICOW073-09
MFNLEP41|Aureopterix_bachmaensis|COI-5P|LR961636			
MFNLEP42|Aureopterix_bachmaensis|COI-5P|LR961637	0.68%		
MICOW073-09|Aureopterix_sterops|COI-5P|HM431791	12.42%	11.79%	
MICOW398-10|Aureopterix_micans|COI-5P|HQ575019	12.77%	11.74%	14.44%

Female genitalia (Fig. 11): segment I to VIII with sclerotized terga and sterna, segment IX elongate, membranous and telescoping, with a continuous sclerotized ring on distal margin, segment X with rounded, lateral sclerites of paired and setose terminal papillae (= papillae anales). (The bursa was completely macerated during boiling in KOH).

Molecular results. (Fig. 2C, Table 1) We recovered only the COI-1a fragment (325bp) for both samples. In the best scoring RAxML-tree the genus *Aureopterix* is well supported as a monophylum with respect to *Zealandopterix* and *Tasmantrix* (BS = 97). Relationships among *A. bachmaensis* sp. nov., *A. micans* and *A. sterops* remain unclear.

Remarks. The locality in the Bach-Ma National Park will probably not remain the only record of this new species. Future field work will provide a more accurate picture of the species range, which is probably restricted to the Truong Son Mountain Range (= Annamite Range). This roughly north to south running mountain range along the Laos-Vietnam border is an area of endemism which gained global recognition in the early to mid-1990s with the discovery of six spectacular mammal species (Sterling and Hurley 2005) that are confined to this range. The report of *A. bachmaensis* sp. nov. in the National Park is an example from Lepidoptera underpinning the significance of the area.

Agathiphagidae

Agathiphagama gen. nov.

http://zoobank.org/0BD622A5-835D-40E1-88EF-A179F51314FD

Type species. *Agathiphagama perdita* sp. nov., Gender: feminine.

Etymology. Composed of the generic name *Agathiphaga* and the added syllable "ma".

Diagnosis. Burmese amber, middle-sized species, terminal segments of maxillary palpi annulated, basal segment of labial palpi with dorsal hair-brush, tibial spurs 1.3.4., epiphysis present on short foretibia, forewings with R1 shortly branched into R1a and R1b, female with long, telescoping ovipositor, apophyses posteriores fused in apical half into a single apophysis extending in midline towards slender papillae anales.

The fossil genus differs from extant homoneurous moths of *Agathiphaga* Dumbleton, 1952 by differences in the morphology of the maxillary and labial palpi, the spur formula 1.3.4. (1.4.4. in *Agathiphaga*) and the long, fused terminal part of the apophyses posteriores (shorter in *Agathiphaga*).

The flexible form of the terminal segment of the maxillary palpi seems to be due to a mottled loss of sclerotization, which gives the segment an annulated appearance. In *Agathiphaga*, this segment is very short and not annulated (Dumbleton 1952).

The new genus is here assigned to Agathiphagidae. An alternative placement considered was the establishment of a new family as sister to Agathiphagidae in Agathiphagoidea. However, there is presently insufficient morphological basis to establish a new family.

Description. See description of *A. perdita* sp. nov. below.

Agathiphagama perdita sp. nov.

http://zoobank.org/0BDBAE24-209D-4838-84B9-CBE96944E77A

Figs 12–17, 32–33

Type material. ***Holotype*** ♀, Burmese amber, NIGP 173715, (NIGP); ***paratype*** ♀, # 7095 (TF).

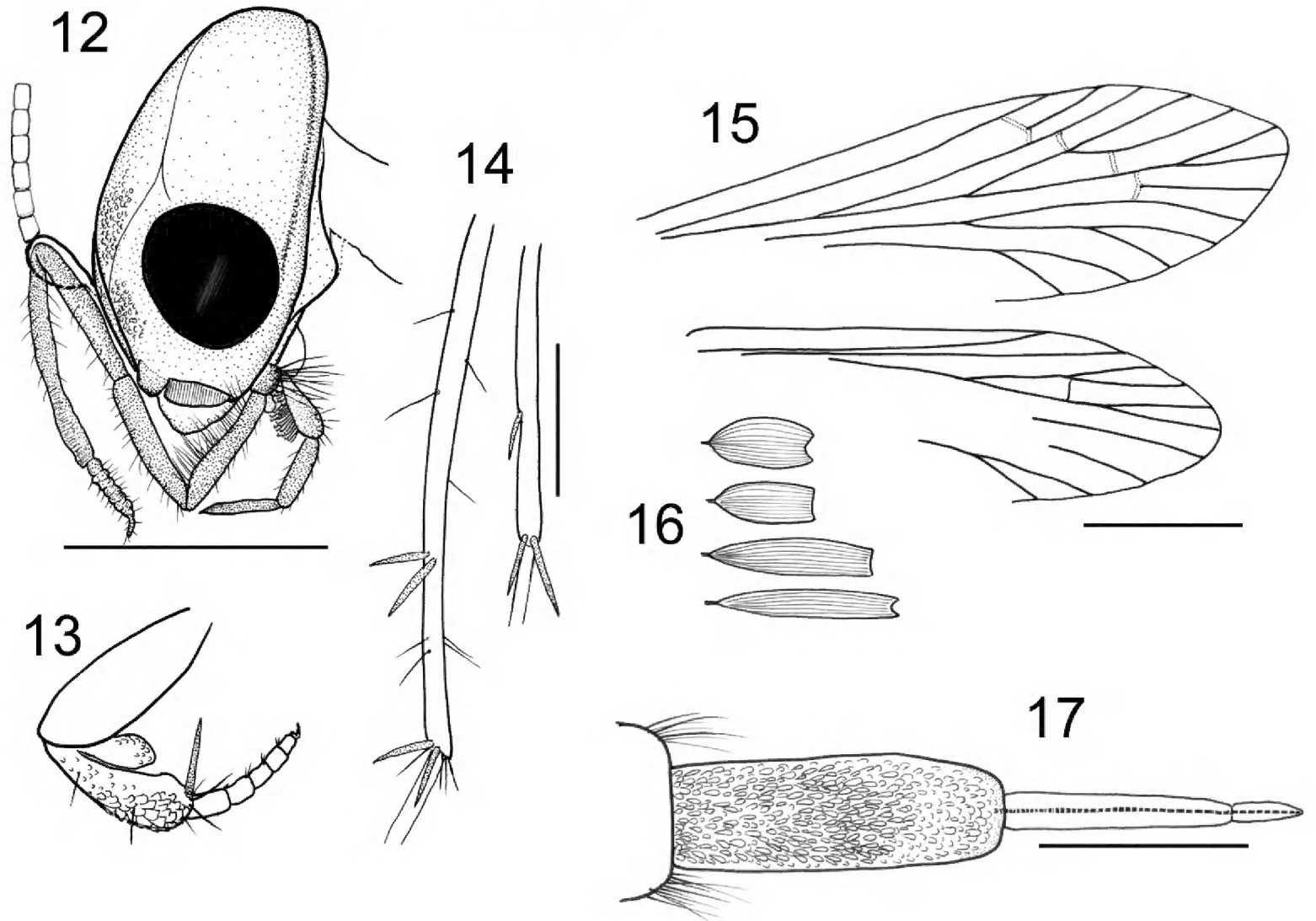
Etymology. The specific name is the Latin adjective "perditus", lost, in singular, feminine nominative, referring to the species as an extinct taxon.

Preservation. The holotype is embedded in a large, polished and oval piece of amber (Fig. 32). The adult insect is nearly completely preserved, somewhat distorted and mainly visible in lateral view. The right side from head to thorax is macerated with right fore- and middle legs missing. The right head side is damaged forming a hole into the head capsule. The hindwings are partly covered by the forewings. One small, black Coleoptera species (3 mm length) is present.

Description. Length of forewings 10.2 mm, head capsule extending far above eyes (Fig. 12), ocelli absent; antennae filiform, longer than 0.5 of forewing length, more than 40 flagellomeres, clothed with small, lamellar scales, scape short, pedicel not larger than following flagellomeres. Maxillary palpi 5-segmented, basal segment with long bristles, terminal segment annulated, labial palpi 3-segmented, dorsal side of basal segment with short, erect, terminally hooked bristles. Foretibia with broad, scaled epiphysis and lateral and apical spines, spurs 1.3.4., meso- and metatibiae with lateral and apical spines (Figs 13, 14). Scales on wings of different shape and length, apical margins with serrations (Fig. 16). Wing venation (Fig. 15) in forewing with Sc simple, R1 shortly branched, accessory cell present, tips of R4 and R5 enclosing apex of forewing, M with four branches; hindwing with unbranched Sc and R1.

Female genitalia (Fig. 17): segment VIII dorso-ventrally flattened, densely covered by short, lamellar scales, segment IX and X forming a long, telescoping oviscapt with unpaired apophysis posterior, visible in the midline of the interior of segments IX and X.

Remarks. This is the first fossil species of the family. It is also the first evidence of the occurrence of the family Agathiphagidae in South-East Asia in the Mesozoic about 100 Ma ago. The morphological differences to *Agathiphaga* are significant and justify at least the establishment of a separate genus. According to Cruickshank and Ko (2003), the palynological record from the Burmese amber mines in northern Myanmar includes palynomorphs of Araucariaceae. Poinar et al. (2007) confirmed the araucarian source of the amber and suggested a species of the genus *Agathis* Salisbury as the resin-producing tree (Poinar 2019b). Extant species can secrete large quantities. Mechanical damage such as cutting into the bark of *A. dammara* (Chambert, 1803) results in large outpourings of resin (Fig. 38). This genus is present in South-East Asia with a number of species occurring in Malaysia and maritime South-East Asia (Michaux 2001). *Agathis* was considered by Morley (1998) as Gondwanan element which dispersed into South East Asia in the Tertiary. The seeds in the fe-



Figures 12–17. *Agathiphagama perdita* gen. nov., sp. nov., female holotype; **12.** Head, lateral view; **13.** Foreleg; **14.** Middle and hind leg; **15.** Wing venation; **16.** Forewing scales; **17.** Postabdomen and oviscapt. Scale bars: 1 mm.

male cones of the trees are the food resource of the two extant species of *Agathiphaga*, *A. vitiensis* Dumbleton, 1952 (Fidji, and further West Pacific Islands) and *A. queenslandensis* Dumbleton, 1952 (Australia, Queensland). The host-plant of *Agathiphagama perdita* sp. nov. could have been also a species of the gymnosperm family Araucariaceae. Judging from the fairly restricted range of *Agathiphaga* in the Australian Region (e.g. Dumbleton 1952) the species seems unlikely to have managed to disperse together with its host-plant into South East Asia. Discrepancy in the distribution of host plants and their associated Lepidoptera species is a frequently observed phenomenon. However, the distribution of herbivorous species is not only determined by the occurrence of the host plant but by the combined action of additional biotic and abiotic factors. Missing data, however, can account as well for a seeming absence in an area. The Microlepidoptera fauna of the region is inadequately researched and new records including surprising discoveries seem to be always possible.

The fossil *Agathiphagama* gen. nov. and the extant *Agathiphaga* are the only genera of Agathiphagidae. Both genera exhibit the characters of the family, but are probably not closely related due to the differences indicated in the diagnosis. The annulated terminal segments of the maxillary palpi of *Agathiphagama* gen.nov. seems to be a derived character. It resembles the terminal maxillary palpi of Annulipalpia and some Integripalpia genera (e.g. *Athripsodes* Billberg, 1820, *Ceraclea* Stephens, 1829) in Trichoptera. Kristensen (2003: 51) considered the annulated surface of the fourth segment as a lepidopteran ground plan character, but this character is not visible in the fossil specimens.

The Agathiphagidae are the only known family in extant Lepidoptera with four veins in the forewings including remarkable variation in branching pattern (Schachat and Gibbs 2016). This plesiomorphic character is, however, present in the Jurassic families Mesokristenseniidae and Ascololepidopterigidae. The former differs from *Agathiphagama* and Agathiphagidae in its spur formula 1.1.4 and in the absence of an epiphysis (Huang et al. 2010). The latter differs from Agathiphagidae and Mesokristenseniidae by lacking medial spurs on the metatibiae (Zhang et al. 2013).

Lophocoronidae

***Acanthocorona* gen. nov.**

http://zoobank.org/238DBF0F-58B8-41BF-B802-C398290772EA

Type species. *Acanthocorona skalskii* sp. nov., Gender: feminine.

Etymology. A noun composed of the Latin "acanthus", thorn and the Latin "corona", crown, alluding to the name *Lophocorona* and to the long spikes at the bases of the valvae and the spine and denticules on its apical margins, forming a spiny crown when the tips of the valvae are hold close together.

Diagnosis. Burmese amber, small-sized species, antennae short, basal flagellomeres broad, epiphysis present, homoneurous venation, forewings with accessory and median cells present, crossvein r1-r2 present, R5 running to termen (below apex) in both wings; valvae of male genitalia with one or more pairs of long, basal spikes and a terminal, short, rod-like 'thorn'.

This fossil genus differs from extant homoneurous moths of *Lophocorona* by the presence of an epiphysis (absent in *Lophocorona*), the presence of crossvein r1-r2 and the joint presence of an accessory and median cell (accessory cell may be present or absent in *Lophocorona*). The valvae in the male genitalia carry a long, rod-like spine on the ventral tip together with numerous short denticules on the apical margin. In *Lophocorona* the spine on the ventral tip is small and blunt. The long spikes originating from the inner side of the base of the valvae can be regarded a synapomorphy of *Lophocorona* and *Acanthocorona* gen. nov.

Description. Forewing length 3–5 mm, eyes hemispherical, frons and vertex with tufts of long piliform scales, ocelli absent; antennae short, about half the length of forewings, about 25–30 flagellomeres present, flagellomeres scaled on dorsal side, wider than long at base, becoming thinner and slender towards tip of antennae; proboscis present, dissociated into galea halves, maxillary palpi reduced in size, labial palpi upturned, terminal segment swollen, densely clothed by short bristles, tibial spurs 0.2.4., spurs covered by small scales, epiphysis present, legs slender (Fig. 26), with thin and strong spines on lateral and apical sides of tibiae, tips of tarsomeres with pair of short spines, ungues and arolium of praetarsus small; forewing venation (Figs 18, 30)) with Sc1 and Sc2, simple R1, sectorial veins of R separate, originating from short accessory cell, R5 terminating to termen shortly below tip of forewing; medial cell present, M4 absent; hindwings (Figs18, 30) with Sc and R1 unbranched, accessory and medial cell open, base of costa with a number of short bristles; scales of forewing short and spatulate, or long with apical margins serrated, scales of fringes long, lanceolate, rounded at apex (Fig. 29).

Male genitalia (Figs 19–27): valvae elongate, band-like, of species-specific shape, with an erect and protruding rod-like, blunt process on ventro-distal corner, directed dorso-mediad, inner side of apical portion or apical margin with short denticules, bases of valvae with one, two or three long spikes, originating from knob-like protuberances or papillae on the inner side; median plate short, of different shape; dorsal median lobe of segment X present or absent, simple or

bifid; phallic apparatus, if extruded, a long, slender tube, sometimes dilated on apex, gonopore in apical position.

Female genitalia (Fig. 31): sternum VIII with broad base and triangular ventral apex; segment IX fused with segment IX, oviscapt cone band-like, dorso-ventrally flattened, strongly sclerotized, fuscous to black, apex blunt, oviscapt saw usually hidden in oviscapt cone, sometimes protruding with its acute tip beyond cone margin.

Remarks. Diagnostic characters of *Lophocorona* Common, 1973 are: 1) absence of an epiphysis, and 2) the long stalk of R4 and R5 in the forewings encompassing the wing apex. These characters are in a plesiomorphic state in *Acanthocorona* gen nov., with epiphysis present and R4 and R5 in the forewings always running as separate veins from accessory cell to wing margin. However, the structures of the male and female genitalia agree largely with those of *Lophocorona*. Especially the architecture of the female postabdomen is very similar to those of females of extant *Lophocorona* species (Nielsen and Kristensen 1996). The nearly complete correspondence of this character complex with *Lophocorona* Common, 1973 provided the clue for identifying specimens in Burmese amber as lophocoronids. A correct association of males and females in Burmese amber is, however, a difficult venture. There are no unique characters other than genitalia, which would permit combining sexes. The structures of the female postabdomen are described in the generic description, but without assigning female specimens to one of the described males.

Burmese amber contains a surprisingly high number of species attributable to *Acanthocorona* gen. nov. The individuals are in most cases embedded in an unfavourable position and exhibit only a reduced number of characters. But none of the externally visible traits contradict the diagnosis and description of the genus. Cross-veins are often difficult to see and they may appear to be absent in some individuals. This uncertainty makes the character unreliable and reduces its taxonomic weight. The following species are described and included in *Acanthocorona* gen. nov. essentially on the basis of the male genitalia. The morphology and arrangements of spines and denticules on apical parts of the valvae constitute the principal character complex, which exhibits a large variety allowing the separation and establishment of different species. The following descriptions of new species are short and concentrate on the male genitalia and their illustrations. The depicted features are diagnostic enough to distinguish the presented species and to identify new species in fresh, additional material of Burmese amber, which hopefully will continue to become available for scientific study in the future.

Acanthocorona skalskii sp. nov.

http://zoobank.org/207948F8-CA26-452C-A09D-D8C0D80F927B

Figs 18–20, 34

Material. ***Holotype*** ♂, Burmese amber, NIGP 173716, (NIGP).

Etymology. The species is named in memory of Andrzej Skalski, who published the first record of a lophocoronid specimen from Asia (Skalski 1979), an interpretation later considered very tentative by Kristensen and Skalski (1998).

Preservation. Completely preserved in a nearly rectangular piece of amber, wings somewhat spread, but overlapping, head, legs and postabdomen clearly visible (Fig. 34).

Description. Length of forewings 4.1 mm, antennae dark brown, with 29 flagellomeres; wing venation (Fig. 18) with cross-veins r1-ac and m-cu present, hindwings without accessory- (ac) and median cell (mc).

Male genitalia (Figs 19, 20): segment IX with short, median prolongation in dorsal view, presumed median plate below this prolongation bilobed; rod-like spine on ventral apex of valvae long and straight, apical margin of valvae with denticules, and some additional denticules before margins; basal spikes of valvae paired, longer as length of valvae, sitting on elongate papillae from median side of valvae, a third median pair of bristles present, shorter than basal spikes. Phallus not visible.

Acanthocorona muelleri sp. nov.

http://zoobank.org/A81F6686-359F-4BCC-AF5E-A0480ABD4BEE

Figs 21, 35, 36

Material. ***Holotype*** ♂, Burmese amber, BUB 1519, (PM).

Etymology. The species is named in honour of Patrick Müller, collector of amber inclusions, for providing material for scientific study.

Preservation. Completely preserved in a flat, oval piece of amber (Fig. 35), wings overlapping, legs and post-abdomen well visible in ventral view, air bubble on mouthparts and prosternum, additional insects present (two Hymenoptera, two Diptera, one Collembola).

Description. Length of forewings 3.0 mm, antennae brown, 23 flagellomeres.

Male genitalia (Figs 21, 36): rod-like spine on ventral apex of valvae long, straight and thickened, apical margin of valvae with three denticules of declining size, no denticles before margins; basal spikes of valvae paired, slightly shorter than length of valvae, arising on elongate papillae at median sides of valvae. Phallus long, tubular and gradually curved ventrad, tip with short, protruding vesica.

Acanthocorona bowangi sp. nov.

http://zoobank.org/0E56BB94-FB95-4A50-A086-5B9EB6451100

Fig. 22

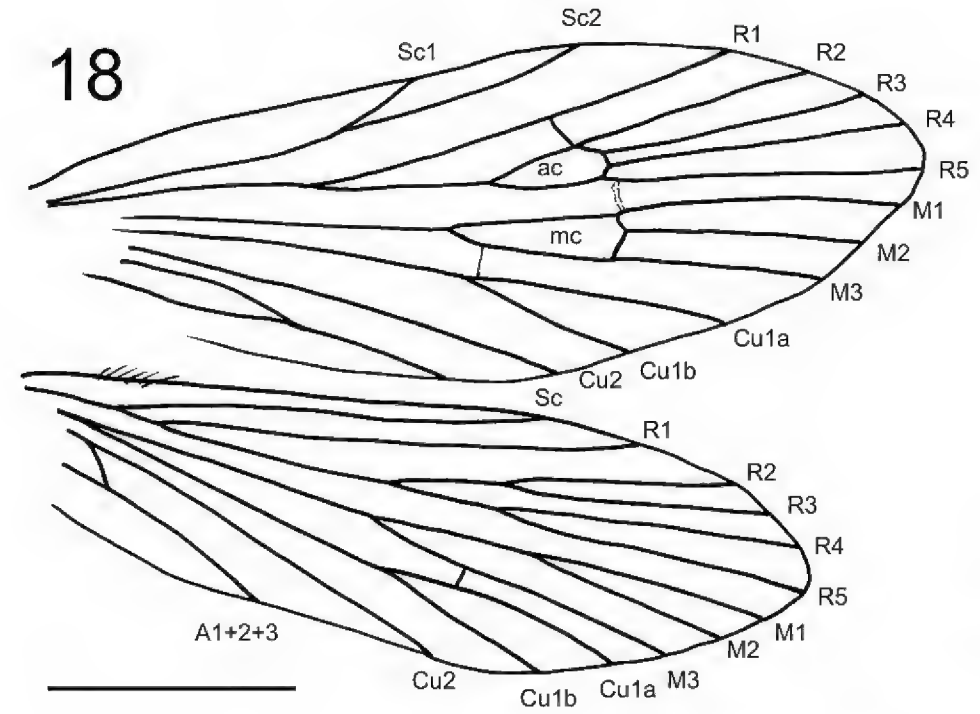
Material. ***Holotype*** ♂, Burmese amber, BUB 1519, (PM).

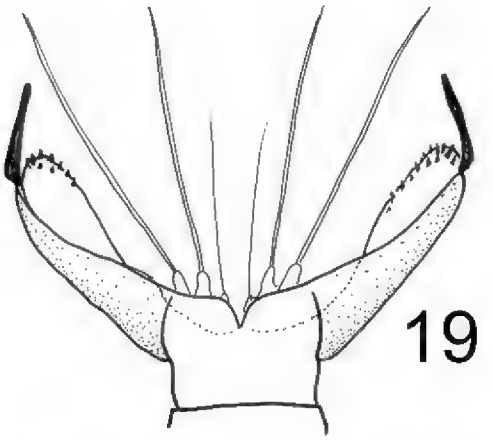
Etymology. The species is named in honour of Bo Wang for his efforts to make Burmese amber material available for scientific study.

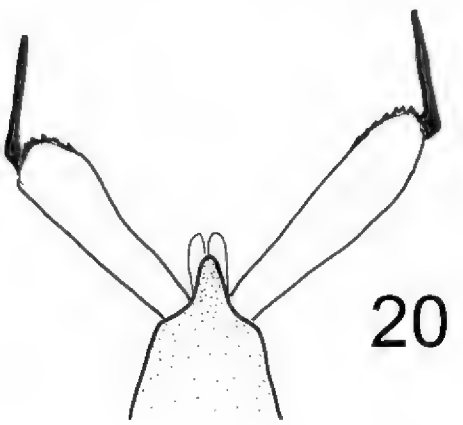
Preservation. Completely preserved on the margin in a large, drop-like piece of amber, wings somewhat overlapping, distorted, legs and post-abdomen clearly visible.

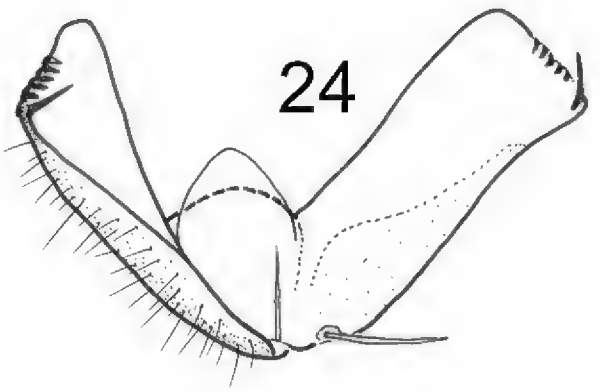
Description. Length of forewings 3.6 mm, antennae dark brown, 24 flagellomeres.

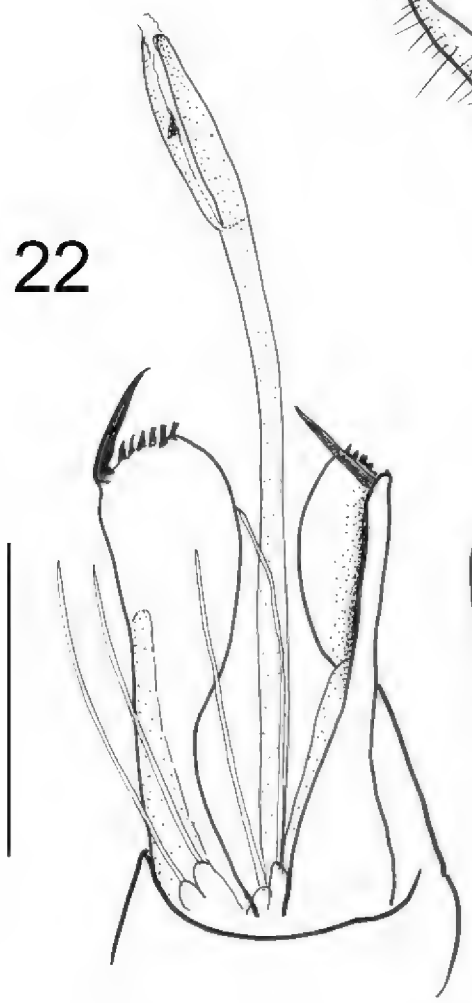
Male genitalia (Fig. 22): length of valvae as long as half the length of abdomen; rod-like spine on ventral apex of valvae long and straight, apical margin of valvae with row of denticules, no denticles before margins; basal spikes of valvae paired, slightly shorter than length of valvae, sitting on elongate papillae from median side of valvae. Phallus extremely long, slightly curved ventrad, ventral side of apex with elongate slit revealing short teeth.

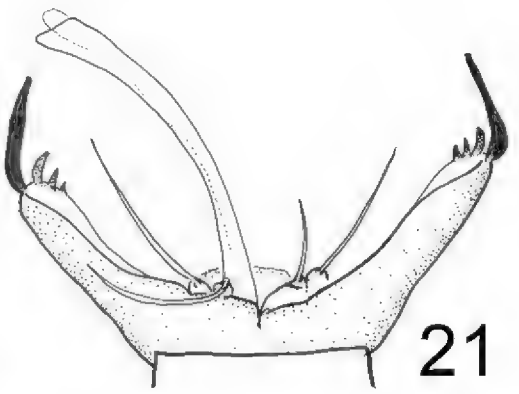


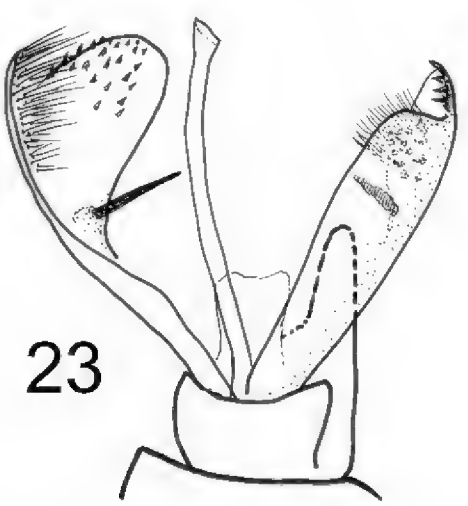




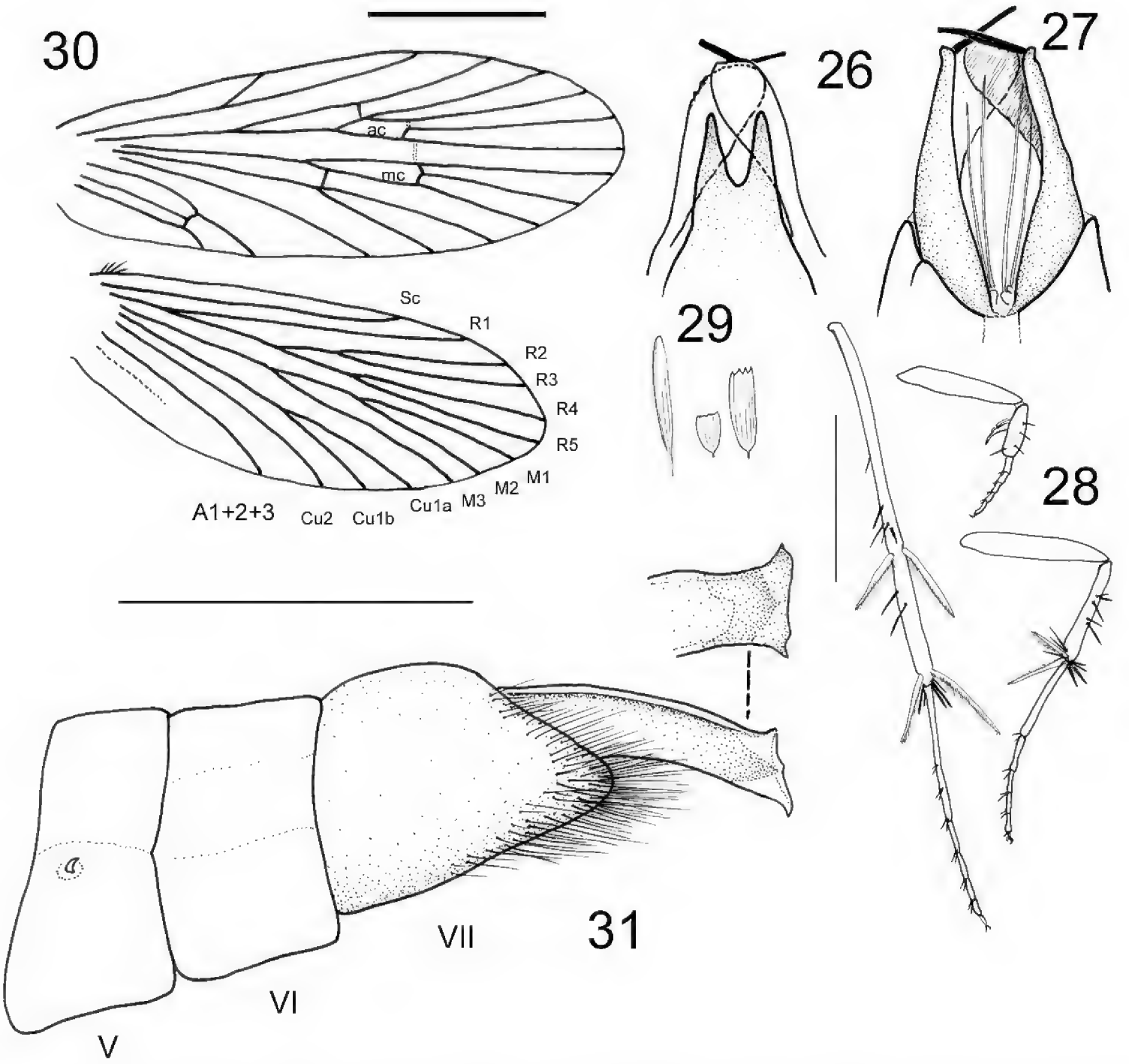








Figures 18–25. *Acanthocorona* spp.: **18–20.** *A. skalskii* sp. nov.: **18.** Wing venation; **19.** Male genitalia, ventral; **20.** Male genitalia, dorsal; **21.** *A. muelleri* sp. nov., male genitalia, ventral, **22.** *A. bowangi* sp. nov., male genitalia, ventral; **23.** *A. wichardi* sp. nov., ventral; **24.** *A. kuranishi* sp. nov., ventro-caudal, **25.** *A. sattleri* sp. nov., male genitalia; A – ventro-lateral, B – dorso-lateral. Scale bars: 1 mm (**18.**); 0.5 mm (**20., 22., 23., 25.**).



Figures 26–31. 26–30. *Acanthocorona spinifera* sp. nov.: **26.** Male genitalia, dorsal; **27.** Ventral; **28.** Legs; **29.** Forewing scales; **30.** Wing venation; **31.** *Acanthocorona* sp., female (NIGP 173719), postabdomen, ventro-lateral view, and oviscapt tip, dorsal view. Scale bars: 0.5 mm (**28.**); 1 mm (**30.**); 0.8 mm (**31.**).

Acanthocorona wichardi sp. nov.

http://zoobank.org/61FB43B8-BD57-4B52-83B1-6D50C4108B1C

Fig. 23

Material. ***Holotype*** ♂, Burmese amber, NIGP 173717 (NIGP).

Etymology. The species is named in honour of Wilfried Wichard for providing material and taking photos of Microlepidoptera of Burmese amber.

Preservation. Completely preserved in an oval piece of amber with much particulate detritus particles and some air bubbles, wings overlapping, legs and post-abdomen clearly visible in ventral

view, one additional insect specimen present (one female of Hydroptilidae, Trichoptera, a single minute Coleoptera).

Description. Length of forewings 3.8 mm, antennae light brown, 24 flagellomeres, long spines on legs absent.

Male genitalia (Fig. 23): segment IX with median prolongation; rod-like spine on ventral apex of valvae absent, replaced by a bulbous area with short and long bristles, apical part of valvae enlarged forming an oval lobe with short denticules of on inner side, no denticles on margins, inner side of valvae with long spine, directed dorso-mediad; basal spikes of valvae absent; median plate short, rectangular in ventral view. Phallus long, tubular and curved ventrad.

Remarks. *A. wichardi* sp. nov. differs from the remaining species of the genus by lacking spines on the legs, absence of basal spikes and apical, rod-like spines of the valvae. The presence of a long spine on the median side of the valvae instead of emerging on the ventral corner is a unique character. The species is provisionally included in the genus until better preserved material becomes available which may lead to a different systematic placement.

Acanthocorona kuranishii sp. nov.

http://zoobank.org/2187398E-84B6-475A-B29D-A390C0062D61

Fig. 24

Material. ***Holotype*** ♂, Burmese amber, MB.I. 5484, (MfN).

Etymology. The species is named in honour of Ryoichi Kuranishi (Chiba, Japan), who generously donated the amber piece with the inclusion to W. Mey and the MfN.

Preservation. Completely preserved in a round, polished piece of amber, but not clearly visible due to several fractures in the amber; numerous small bubbles of air present; wings overlapping, legs and postabdomen clearly visible.

Description. Length of forewings 4.0 mm, antennae light brown, 25 flagellomeres, legs with strong spines.

Male genitalia (Fig. 24): segment IX with short,triangular, median prolongation in ventro-caudal view; rod-like spine on ventral apex of valvae short, apical margin of valvae with row of five denticules, no denticules on inner side before margins; one pair of basal spikes of valvae present, about 1/3 the length of valvae. Phallus not visible.

Acanthocorona sattleri sp. nov.

http://zoobank.org/5638DDFF-C5C3-4592-B8CC-A5EEF7F1B935

Fig. 25A, B

Material. ***Holotype*** ♂, Burmese amber, BUB 570, (PM); paratype ♂, Burmese amber, James Ziegras Collection, JZC – Bu 203 (AMNH).

Etymology. The species is named in honour of Klaus Sattler, London, specialist of Microlepidoptera in the Natural History Museum, London, for his support and help during many visits of the first author to the Microlepidoptera collection in London.

Figure 32. *Agathiphagama perdita* gen. nov., sp. nov., female holotype.

Figure 33. *Agathiphagama perdita* gen. nov., sp. nov., female holotype, photographed submerged in glycerine.

Figure 34. *Acanthocorona skalskii* sp. nov., male holotype, ventral view.

Figure 35. *Acanthocorona muelleri* sp. nov, male holotype, ventral view.

Preservation. Completely preserved in a flat, rounded and polished piece of amber, numerous small bubbles of air and two, minute midges (Diptera) present; wings overlapping, head, legs and postabdomen clearly visible in ventral view.

Description. Length of forewings 2.9 mm, antennae light brown, very short, about 0.3 of forewing length, with 21 flagellomeres.

Male genitalia (Fig. 25): segment IX rounded dorsally, segment X with short, bifid median prolongation in latero-dorsal view (Fig. 25A); rod-like spine long, accompanied by shorter spines on ventral apex of valvae, apical margin of valvae with row of denticules, additional denticules before margins; basal spikes of valvae paired, about half the length of valvae (Fig. 25B). Phallus not extruded.

Acanthocorona spinifera sp. nov.

http://zoobank.org/F1BCDBB6-57DD-4486-8EC3-7B3D35A375F5

Figs 18, 26–30, 37

Material. ***Holotype*** ♂, Burmese amber, NIGP 173718, (NIGP).

Etymology. The specific epithet is composed from Latin "spina", spine, and "fero", to carry, referring to the strong spines on tibiae of the adult moth.

Preservation. Completely preserved in a small, rounded, polished piece of amber, embedded in dorso-ventral position, with right wings spread out, some short fractures and few a bubbles of air present, legs and postabdomen well visible (Fig. 37).

Description. Length of forewings 4.8 mm, antennae dark brown, less than 0.5 of forewing length, with 30 flagellomeres; scales of forewing short and spatulate, or long with apical margin serrated, scales of fringes long, lanceolate, rounded at apex (Fig. 29).

Male genitalia (Figs 27, 28): segment X a large dorsal plate with deep, triangular excision of apical margin giving the structure a bifid form (Fig. 28); valvae broad, somewhat enlarged and rounded on apices; rod-like spine on ventral apex of valvae long, apically truncate, not accompanied by shorter spines, apical margin of valvae without denticules, basal spikes of valvae paired, about 0.8 the length of valvae (Fig. 27). Phallus not extruded.

Acanthocorona sp.

Fig. 31

Material. 1 ♀, Burmese amber, NIGP 173719, (NIGP); 1 ♀, # 7098 (TF).

Description. Length of forewings 3.4–4.2 mm, antennae pale brown, about 0.3 of forewing length, with 22–25 flat flagellomeres; labial palpi larger than maxillary palpi, terminal segment bulbous with long bristles, proboscis small; epiphysis present, legs with spines and scaled spurs; wing venation homoneurous, R5 to termen.

Female genitalia (Fig. 31): sternum VIII with broad base and triangular ventral apex; segment IX fused with segment IX, oviscapt cone band-like, dorso-ventrally flattened, strongly sclerotized,

Figure 36. *Acanthocorona muelleri* sp. nov., close-up of male genitalia, ventral view.

Figure 37. *Acanthocorona spinifera* sp. nov., male holotype, ventral view.

Figure 38. Old tree of *Agathis dammara* (Chambert, 1803) in the forest of Mt. Salak-Halimun National Park (Java) with resin secretion; **A.** Basal trunk with several outpourings; **B.** Close-up of an outpouring caused by mechanical damage (photo: W. Mey).

fuscous to black, apex blunt, oviscapt saw usually hidden in oviscapt cone, sometimes protruding with its acute tip beyond cone margin.

Remarks. These female specimens cannot be assigned to any of the named species at the moment (see under remarks in the genus description). Since the female genitalia is an important character complex for the recognition of the family, the genitalia of one individual (NIGP 173719) was illustrated. The genitalia of the second species are difficult to see but are identifiable as those of a female.

Discussion

This paper aims to complete the picture of the distribution and diversity of past and recent primitive moths. A formal biogeographic analysis or providing a comprehensive review of recent and past distributions was beyond the scope of this study. The following discussion aims to guide any future biogeographical studies on primitive moths of South-East Asia, as well as to foster further works on Lepidoptera fossils.

1. *Aureopterix bachmaensis* sp. nov.

Wagner and Davis (2014) discovered Neotropical taxa of Micropterigidae occurring in Costa Rica and reported the first example of a genus range in the family stretching over both sides of the Equator (*Squamicornia*). *Aureopterix* is now another example of a micropterigid genus with records from the Northern and Southern Hemisphere, but in this case, oceans divide the disjunct parts of the generic range. The distance between the disjunct ranges of *A. bachmaensis* and the other two known species is about 6000 km on a northwest-southeast axis. Knowledge of the microlepidopteran fauna of the Larger and Smaller Sunda Islands as well as of New Guinea is poor, and thus we cannot exclude the possible occurence of Micropterigidae in these regions. The notion of a continuous distribution of *Aureopterix* in the Indo-Australian Archipelago, today or in the past was our initial hypothesis, considering the many documented examples of this distribution type in Lepidoptera (Holloway 1998; Holloway and Nielsen 1998; Holloway et al. 2001; De Jong 2001).

Dispersal and colonization processes are closely related to the tectonic structure and geological and climate history in South East Asia, Melanesia and the Southwest Pacific. Kitching et al. (2001) and De Jong (2001) analysed the distribution pattern of butterflies and suggested a number of hypotheses which are synthetical explanations including tectonic, evolutionary and ecological processes with dispersal as important mechanism. In contrast to butterflies, thought to have originated around 119 Ma ago (Espeland et al. 2018) primitive homoneurous families of Lepidoptera are much older and have already existed during periods of tectonic movements 180 Ma ago in the Early Jurassic (Ansorge 2002; Grimaldi and Engel 2005). The basal splitting event among known extant Lepidoptera is presumed to have given rise to the Micropterigidae (Kristensen and Skalski 1998; Wahlberg et al. 2013; Regier et al. 2015; Kawahara et al. 2019) and its sister group, the bulk of the Lepidoptera. The family has a widely scattered cosmopolitan distribution, which might suggest a Pangaean origin. In a continental drift scenario and/or any relevant independent dating, disjunct distribution patterns in this family can also be explained by providing vicariance-driven scenarios based on tectonic history reaching back into the Mesozoic. Recently, for example, Grehan and Mielke (2018, 2020) proposed such a vicariance model for explaining the distribution of the homoneurous Hepialoidea in the Southwest Pacific area.

In a molecular study of the radiation of the micropterigid genus *Sabatinca* Walker, 1863 in New Caledonia and New Zealand using COI-5P, both species of *Aureopterix* known for the Australian region were included (Gibbs and Lees 2014). According to the dating analysis of these authors based also on fossil calibrations, the Australia-New Caledonia split in *Aureopterix* is ca. 54 Ma old (95% interval: 40–74 Ma) and the branching of *Aureopterix* and *Zealandopterix* in their chronogram was estimated at ca. 83 Ma (95% confidence interval: 62–102 Ma). These dates substantially postdate the timing of the breakup of East Gondwana into Madagascar+India and into Australia, New Zealand and Antarctica at ca. 130 Ma based on palaeomagnetic dates (McIntyre et al. 2017), after the presumed detachment of terranes from northern Gondwana predicted from its geology at ca. 120 Ma (Metcalfe 2001, 2017). Thus, the vicariance scenarios are not in agreement with the age and phylogeny-based divergence times of *Aureopterix* and related taxa as documented in Gibbs and Lees (2014), who also noted such a conflict in the split of *A. micans* and *A. sterops*. If this phylogenetic dating is accurate, we have to consider alternative, dispersal processes as the main driver in shaping the disjunct range of *Aureopterix*, rather than passive transport on continental terranes or vicariance via submerged parts of ancient continents. The recovering of *Aureopterix* within a clade including the stricly Australasian genera *Tasmantrix* and *Zealandopterix* suggests an Australasian origin of *Aureopterix*, with a long-distance dispersal for *A. bachmaensis* being the most probable scenario. The discovery of this genus in Vietnam is remarkable since the overseas dispersal scenario is rather hard to imagine because these taxa are moist forest dwellers, essentially confined to the substratum with larvae and adults highly prone to desiccation when leaving their habitats (Lorenz 1961). The biology of *Aureopterix* is not known yet, but host plant were shown to be strictly conserved in Micropterigidae of Japan, all feeding on the liverwort *Conocephalum conicum*. Gibbs and Lees (2014) also acknowledged a weak dispersal power in Micropterigidae. There might be other dispersal mechanisms we are unaware of, or the geological history of continental terranes, including the context with neighbouring oceanic islands or island arcs seem to be imperfectly known to date (for example geological uncertainties about submerged continents such as in the Australian region Zealandia), or both.

2. Agathiphagidae, Lophocoronidae

The stunning discovery of extinct taxa of primitive Lepidoptera in Myanmar, which were thought to be restricted in their distribution to the Australian Region, substantially revises present notions on the historical biogeography of Lepidoptera groups. In the absence of fossil distributions, Agathiphagidae and Lophocoronidae seem like classic cases of endemism in the Australian Region. *Agathiphaga* has two known species and stretches across the Pacific to Solomons, Vanuatu and Fiji and is thought to have benefitted from the possibility of long diapause in drifting *Agathis* seeds (Upton 1994). The biology of *Lophocorona*, by contrast, is still unknown. The fossil species of Agathiphagidae and Lophocoronidae found in Myanmar might alternatively provide evidence of a wider ancestral distribution of the two families, if such oceanic dispersal mechanisms do not prove to be a significant transport mechanism. The hypothesis that their extant ranges in the southern Hemisphere are relicts of a previous intercontinental distribution encompassing Asia and Australia has not yet been tested.

The time of divergence for lineages leading to the families Agathiphagidae and Eriocraniidae+Lophocoronidae was estimated by Wahlberg et al. (2013) at around 160 Ma (Agathiphagidae) and at around 180 Ma (Eriocraniidae+Lophocoronidae). At this time, in the Early to Late Jurassic, the distribution and positions of continents were quite different from their configuration today. The increasing

separation of Laurasia and Gondwana by the Tethys ocean occurred in the Jurassic and was completed in the Cretaceous (Metcalfe 2017). This long period in earth history allows for proposing hypotheses which explain present distribution patterns in terms of passive transport on continental plates.

From a historical perspective, the Oriental fauna is a mixture of tropical Laurasian and Gondwanan taxa, over which is overlaid the results of dispersal processes. The collision of the Indian subcontinent into Asia in the early Eocene brought elements of the Gondwana fauna to the north and resulted in a pronounced enrichment of the biota (Morley 1998). Long before the accretion of India, several terranes were detached from the margin of North-East Gondwana and were shifted to the north during the Jurassic. They arrived at Laurasia and became part of the Asian continent during the Cretaceous (Metcalfe 2017). With the movement of these continental terranes, ancient biota could have been transported, and given permanent over-water conditions of the terranes during the passage, arrived in Asia and immigrated into the resident biota. Based on this geological scenario, the extant occurrence and distribution of the Gondwanan caddisfly family Hydrobiosidae (Trichoptera) in Asia were explained by a vicariance/dispersal model (Mey 1998). Further examples of this terrane transport from angiosperms and invertebrate groups with disjunct ranges in Asia and Australia were provided by Poinar (2019b), underpinning the explanatory value of this model of shifting terranes. The occurrences of Agathiphagidae and Lophocoronidae during the Mesozoic in Asia can be explained likewise as a result of a transport by northward drifting Gondwana terranes. So far there have been practically no molecular or other analyses that might seriously test such models.

Acknowledgements

Our thanks go to Bo Wang (Nanjing, Beijing), R. Kuranishi (Chiba), P. Müller (Käshofen), T. Fischer (Munich) and W. Wichard (Bonn) for providing material of Burmese amber. Robert Schreiber (Museum für Naturkunde, Berlin) performed the PCR and processed samples for sequencing. The map was prepared by Jürgen Mey. Photos of species in Burmese amber inclusions were taken by W. Wichard (Bonn). Maria Heikkilä (Helsinki) provided photos of *Acanthocorona* species from the AMNH, New York.

The participation of the first author in the VIETBIO project including field work in Vietnam was generously supported by the Museum für Naturkunde, Berlin, and the German project leaders C. Häuser and T. von Rintelen.

We thank J. Dunlop (Berlin) and David C. Lees for valuable suggestions on drafts of the manuscript and for correcting the English text. G. W. Gibbs (Wellington), J. Minet (Paris), M. Kozlov (Turku) and an anonymous reviewer are thanked for their constructive corrections and hints. The project is supported by the German Federal Ministry of Education and Research (BMBF) since 2017 (grant ID: 01 DP17052).

References

Ansorge J (2002) Revision of the "Trichoptera" described by Gleinitz and Handlirsch from the Lower Toarcian of Dobbertin (Germany) based on new material. In: Mey W (Ed.) Proceedings of the 10th International Symposium on Trichoptera, Potsdam, Germany 2000. Nova Supplementa Entomologica 15**:** 55–74.

Balian EV, Lévêque C, Segers H, Martens K (2008) Freshwater animal diversity assessment. Hydrobiologia 595(1): 627–637. https://doi.org/10.1007/s10750-007-9246-3

Barthlott W, Kier G, Mutke J (1999) Globale Artenvielfalt und ihre ungleiche Verteilung. Courier Forschungsinstitut Senckenberg 215: 7–22.

Cockerell TDA (1919) Two interesting insects in Burmese amber. The Entomologist 52 (676): 193–195.

Chen L, Owada M, Wang M, Long Y (2009) The genus *Neopseustis* (Lepidoptera: Neopseustidae) from China, with description of one new species. Zootaxa 2089: 10–18. https://doi.org/10.11646/zootaxa.2089.1.2

Common IFB (1973) A new family of Dacnonypha (Lepidoptera) based on three new species from southern Australia, with notes on the Agathiphagidae. Journal of the Australian Entomological Society 12: 11–23. https://doi.org/10.1111/j.1440-6055.1973.tb02150.x

Cruickshank RD, Ko K (2003) Geology of an amber locality in the Hukawng Valley, Northern Myanmar. Journal of Asian Earth Sciences 21: 441–455. https://doi.org/10.1016/S1367-9120(02)00044-5

Davis DR, Karsholt O, Kristensen NP, Nielsen ES (1995) Revision of the genus *Orgygioses* (Palaeosetidae). Invertebrate Taxonomy 9: 1231–1263. https://doi.org/10.1071/IT9951231

De Jong R (2001) Faunal exchange between Asia and Australia in the Tertiary as evidenced by recent butterflies. In: Metcalf I, Smith JMB, Morewood M, Davidson I (Eds) Faunal and floral migrations and evolution in SE Asia-Australasia, A.A. Balkema Publishers Lisse, 133–146.

Dumbleton LJ (1952) A new genus of seed infesting micropterygid moths. Pacific Science 6: 17–29.

Espeland M, Breinholt J, Willmott KR, Warren AD, Vila R, Toussant EFA, Maunsell MC, Aduse-Poku K, Talavera G, Eastwood R, Jarzyna MA, Guralnick R, Lohman DJ, Pierce NE, Kawahara AY (2018) A comprehensive and dated phylogenomic analysis of butterflies. Current Biology 28: 770–778. https://doi.org/10.1016/j.cub.2018.01.061

Fjeldså J, Lovett JC (1997) Biodiversity and environmental stability. Biodiversity and Conservation 6: 315–323. https://doi.org/10.1023/A:1018304522320

Gibbs GW (2010) Micropterigidae (Lepidoptera) of the southwestern Pacific: a revision with the establishment of five new genera from Australia, New Caledonia and New Zealand. Zootaxa 2520: 1–48. https://doi.org/10.11646/zootaxa.2520.1.1

Gibbs GW, Lees DC (2014) New Caledonia as an evolutionary cradle: a re-appraisal of the jaw-moth genus *Sabatinca* (Lepidoptera; Micropterigidae) and its significance for assessing the antiquity of the island's fauna. In: Guilbert E, Robillard T, Jourdan H, Grandcolas P (Eds) Zoologia Neocaledonica 8. Biodiversity studies in New Caledonia. Muséum nationale d'Histoire naturelle, Paris, 239–266.

Grehan JR, Mielke CGC (2018) Evolutionary biogeography and tectonic history of the ghost moth families Hepialidae, Mnesarchaeidae, and Palaeosetidae in the Southwest Pacific (Lepidoptera: Exoporia). Zootaxa 4415(2): 243–275. https://doi.org/10.11646/zootaxa.4415.2.2

Grehan JR, Mielke CGC (2020) Taxonomic revision and biogeography of *Phassodes* Bethune-Baker, 1905 (Lepidoptera: Hepialidae), ghost moth descendants of a subduction zone weed in the south-west Pacific. Bishop Museum Occasional Papers 136: 1–37.

Grimaldi D, Engel MS (2005) Evolution of the insects. Cambridge University Press, [XV +] 755 pp.

Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361: 1–72. https://doi.org/10.1206/0003-0082(2002)361%3C0001:FCAFMB%3E2.0.CO;2

Hashimoto S, Mey W (2000) Establishment of a new genus *Vietomartyria* (Lepidoptera, Micropterigidae) for *Paramartyria expeditionis* Mey. Transactions of the Lepidopterological Society of Japan 52: 37–44.

Hirowatari T, Hashimoto S, Jinbo U, Wang M (2009) Description of two new species of *Vietomartyria* Hashimoto & Mey (Lepidoptera, Micropterigidae) from South China, with reference to autapomorphies of the genus. Entomological Science 12: 67–73. https://doi.org/10.1111/j.1479-8298.2009.00305.x

Holloway JD (1998) Geological signal and dispersal noise in two contrasting insect groups in the Indo-Australian tropics: R-mode analysis of pattern in Lepidoptera and cicadas. In: Hall R, Holloway JD (Eds) Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, 291–314.

Holloway JD, Nielsen ES (1998) Biogeography of the Lepidoptera. In: Kristensen NP (Ed.) Lepidoptera, Moths and Butterflies, vol. 1, Evolution, Systematics, and Biogeography. Handbuch der Zoologie Bd. IV, Teilband 35, 423–462.

Holloway JD, Kibby G, Peggie D (2001) The families of Malesian moths and butterflies. Fauna Malesiana Handbook 3, 455 pp.

Huang D, Nel A, Minet J (2010) A new family of moths from the Middle Jurassic (Insecta: Lepidoptera). Acta Geologica Sinica 84(4): 874–885. https://doi.org/10.1111/j.1755-6724.2010.00233.x

Hwang CL (1965) A new genus and species of Mnesarchaeidae (Lepidoptera: Eriocranioidea). Acta Zootaxonomica Sinica 2(1): 33–36.

Imada Y, Kawakita A, Kato M (2010) Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera, Micropterigidae). Proceedings of the Royal Society B 278: 3026–3033. https://doi.org/10.1098/rspb.2011.0134

Issiki ST (1931) On the morphology and systematics of Micropterygidae (Lepidoptera: Homoneura) of Japan and Formosa, with some considerations on the Australian, the European and North American forms. Proceedings of the Zoological Society, London 1931: 999–1039. https://doi.org/10.1111/j.1096-3642.1931.tb01052.x

Issiki ST, Stringer H (1932) On new oriental genera and species of the Hepialoidea (Lepidoptera: Homoneura). Stylops 1: 71–72. https://doi.org/10.1111/j.1365-3113.1932.tb01354.x

Kawahara AY, Plotkin D, Espeland M, Meusemann K, Toussaint EF, Donath A, Barber JR (2019) Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Proceedings of the National Academy of Sciences 116(45): 22657–22663. https://doi.org/10.1073/pnas.1907847116

Konstantinov AS, Korotyaev BA, Volkovitsh MG (2009) Insect biodiversity in the Palearctic Region. In: Foottit RG, Adler PH (Eds) Insect biodiversity: science and society. Wiley-Blackwell, 107–162. https://doi.org/10.1002/9781444308211.ch7

Kristensen NP, Skalski A (1998) Phylogeny and palaeontology. In: Kristensen NP (Ed.) Lepidoptera, Moths and Butterflies, vol. 1, Evolution, Systematics, and Biogeography. Handbuch der Zoologie Bd. IV, Teilband 35, 7–25.

Kristensen, NP (1998) The non-glossatan moths. In: Kristensen NP (Ed.) Lepidoptera, Moths and Butterflies, vol. 1, Evolution, Systematics, and Biogeography. Handbuch der Zoologie Bd. IV, Teilband 35, 41–49.

Kristensen NP (2003) Skeleton and muscles: adults. In: Kristensen NP (Ed.) Lepidoptera, Moths and Butterflies, vol. 2, Morphology, Physiology and Development. Handbuch der Zoologie Bd. IV, Teilband 36, 39–131.

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Lees DC, Rougerie R, Zeller-Lukashorst C, Kristensen NP (2010) DNA mini-barcodes in taxonomic assignment: a morphologically unique new homoneurous moth clade from the Indian Himalayas described in *Micropterix* (Lepidoptera, Micropterigidae). Zoologica Scripta 39: 642–661. https://doi.org/10.1111/j.1463-6409.2010.00447.x

Léger T, Kehlmaier C, Vairappan CS, Nuss M (2020) Twenty-six new species of *Hoploscopa* (Lepidoptera, Crambidae) from South-East Asia revealed by morphology and DNA barcoding. Zookeys 907: 1–99. https://doi.org/10.3897/zookeys.907.36563

Lorenz RE (1961) Biologie und Morphologie von *Micropterix calthella* (L.) (Lep. Micropterygidae [sic]). Deutsche Entomologische Zeitschrift, Neue Folge 8(1–2): 1–23. https://doi.org/10.1002/mmnd.4800080104

McIntyre SRN, Lineweaver CH, Groves CP, Chopra A (2017) Global biogeography since Pangaea. BioRxiv preprint. https://doi.org/10.1101/146142

Metcalfe I (2001) Palaeozoic and Mesozoic tectonic evolution and biogeography of SE Asia-Australasia. In: Metcalfe I, Smith, JMB, Morewood M, Davidson I (Eds) Faunal and floral migrations and evolution in SE Asia-Australasia. A.A. Balkema Publishers Lisse, 15–34.

Metcalfe I (2017) Tectonic evolution of Sundaland. Bulletin of the Geological Society of Malaysia 63: 27–60. https://doi.org/10.1101/146142

Mey W (1997) Moths of Vietnam with special reference to Mt. Fan Si Pan. Microlepidoptera 1: Micropterigidae/Urmotten, Lepidoptera, Zeugloptera). Entomofauna (Ansfelden) Supplement 9: 13–20.

Mey W (1998) The distribution of *Apsilochorema* Ulmer, 1907: biogeographic evidence for the Mesozoic accretion of a Gondwana microcontinent to Laurasia. In: Hall R, Holloway JD (Eds) Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, 91–98.

Mey W (2019) Microlepidoptera in Burmese Amber (Insecta, Lepidoptera). DGaaE-Nachrichten 33(2): 85–86.

Mey W, Häuser C, Lien VV (2020) On the Microlepidoptera of the Bach-Ma National Park in Central Vietnam (Insecta, Lepidoptera). Mitteilungen der DGaaE 22: 165–169.

Meyrick E (1909) Descriptions of Indian Microlepidoptera. Journal of the Bombay Natural History Society 19(2): 410–437.

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: 2010 Gateway Computing Environments Workshop (GCE). New Orleans, LA, 1–8. https://doi.org/10.1109/GCE.2010.5676129

Morley RJ (1998) Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In: Hall R, Holloway JD (Eds) Biogeography and geological evolution of SE Asia. Backhuys Publishers, Leiden, 211–234.

Müller J, Müller K, Neinhuis C, Quandt D (2005) PhyDE-Phylogenetic Data Editor. http://www.phyde.de/

Müller P (1981) Arealsysteme und Biogeographie. Eugen Ulmer, Stuttgart, 704 pp.

Mutuura A (1971) A new genus of a homoneurous moth and the description of a new genus (Lepidoptera: Neopseustidae). The Canadian Entomologist 103: 1129–1136. https://doi.org/10.4039/Ent1031129-8

Nielsen ES, Kristensen NP (1996) The Australian moth family Lophocoronidae and the basal phylogeny of the Lepidoptera-Glossata. Invertebrate Taxonomy 10: 1199–1302. https://doi.org/10.1071/IT9961199

Poinar Jr G, Lambert JB, Wu Y (2007) Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. Journal of the Botanical Research Institute of Texas 1(1): 449–455. https://www.biodiversitylibrary.org/page/34395560

Poinar Jr G (2019a) A new genus of moths (Lepidoptera: Gracillarioidea: Douglasiidae) in Myanmar amber. Historical Biology 31(7): 898–902. https://doi.org/10.1080/08912963.2017.1402016

Poinar Jr G (2019b) Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. Historical Biology 31(10): 1304–1309.

Regier JC, Mitter C, Kristensen NP, Davis DR, Van Nieukerken E, Rota J, Simonsen T, Mitter KT, Kawahara AY, Yen SH, Cummings MP, Zwick A (2015) A molecular phylogeny for the oldest (nonditrysian) lineages of extant Lepidoptera, with implications for classification, comparative morphology and life-history evolution. Systematic Entomology 40(4): 671–704. https://doi.org/10.1111/syen.12129

Robinson GC (1976) The preparation of slides of Lepidoptera genitalia with special reference to the Microlepidoptera. Entomologist`s Gazette 27: 127–132.

Ross AJ (2020) Supplement to the Burmese (Myanmar) amber checklist and bibliography, 2019. Palaeoentomology 3(1): 103–118. https://doi.org/10.11646/palaeoentomology.3.1.14

Schachat SR, Gibbs GW (2016) Variable wing venation in *Agathiphaga* (Lepidoptera: Agathiphagidae) is key to understanding the evolution of basal moths. Royal Society open Science 3(10): e160453. https://doi.org/10.1098/rsos.160453

Shi G, Grimaldi DA, Harlow, GE, Wang J, Wang Y, Yang M, Le W, Li Q, Li X (2012) Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Skalski AW (1979) Records of oldest Lepidoptera. Nota Lepidopterologica 2(1–2): 61–66.

Sohn JC, Labandeira C, Davis DR, Mitter C (2012) An annotated catalogue of fossil and subfossil Lepidoptera (Insecta, Holometabola) of the world. Zootaxa 3286**:** 1–132. https://doi.org/10.11646/zootaxa.3286.1.1

Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22(21): 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Sterling EJ, Hurley MM (2005) Conserving biodiversity in Vietnam: applying biogeography to conservation research. Proceedings of the California Academy of Sciences 56, supplement 1(9): 98–114.

Upton MS (1997) A twelve-year larval diapause in the Queensland kauri moth, *Agathiphaga queenslandiae* Dumbleton (Lepidoptera: Agathiphagidae). The Entomologist 116: 142–143.

Wagner DL, Davis DR (2014) First report of the family Micropterigidae (Lepidoptera) from Central America, with the discovery of two new genera and five new species. Entomological society of America Annual Meeting 2014, Conference paper (published abstract). https://esa.confex.com/esa/2014/webprogram/Paper88117.html

Wahlberg N, Wheat CW, Peňa C (2013) Timing and patterns in the taxonomic diversification of Lepidoptera (butterflies and moths). PLoS ONE 8(11): e80875. https://doi.org/10.1371/journal.pone.0080875

Zhang W-T, Shih, C-K, Labandeira CC, Sohn JC, Davis DR, Santiago-Blay JA, Flint O, Ren D (2013) New fossil Lepidoptera (Insecta. Amphiesmenoptera) from the Middle Jurassic Jiulongshan Formation of northeastern China. PLoS ONE 8(11): e79500. https://doi.org/10.1371/journal.pone.0079500

Zhang W-T, Wang J-J, Shih CK, Ren D (2017) Cretaceous moths (Lepidoptera: Micropterigidae) with preserved scales from Myanmar amber. Cretaceous Research 78: 166–173. https://doi.org/10.1016/j.cretres.2017.06.016